Tropical Ecology **46**(1): 99-111, 2005 ISSN 0564-3295

Tree condition and natural regeneration in disturbed sites of Bwindi Impenetrable Forest National Park, southwestern Uganda

GERALD EILU[1] & JOSEPH OBUA

Department of Forest Biology and Ecosystems Management, Makerere University,
P.O. Box 7062, Kampala, Uganda

Abstract: Tree condition and characteristics of natural regeneration of tree species was assessed in Bwindi Impenetrable National Park. Sampling was done in anthropogenically undisturbed, lightly disturbed, heavily disturbed and completely disturbed forest types. Nested plots measuring 25 x 30 m were established to assess tree size classes from seedlings (diameter < 2 cm and height ≤ 150 cm) to large trees (DBH > 15 cm). Higher stem densities were found in undisturbed and lightly disturbed forest types compared to heavily or completely disturbed types. Tree species richness and diversity were highest in lightly disturbed forest. *Acacia mearnsii,* an introduced tree species in Uganda, was recorded in completely disturbed forest. Regeneration from vegetative sprouts was highest in disturbed sites while regeneration from seeds was highest in undisturbed sites. High intensity human disturbance was associated with fewer signs of mammal damage. Damage to trees by physical agents and climber abundance increased with intensity of disturbance except in completely disturbed forest. High intensity human disturbance adversely affected tree species abundance, diversity and regeneration and increased the incidence of damage to trees. Regeneration from vegetative sprouts was most important in heavily disturbed sites. Intensity of disturbance and slope influenced the distribution of regenerating tree species.

Resumen: La condición de los árboles y las características de la regeneración natural de especies arbóreas fueron evaluadas en el Parque Nacional del Bosque Impenetrable Bwindi. El muestro se llevó a cabo en tipos de bosque sin perturbación, ligeramente perturbado, fuertemente perturbado y completamente perturbado. Se establecieron parcelas anidadas de 25 × 30 m con el fin de evaluar las clases de tamaño de los árboles desde plántulas (diámetro < 2 cm y altura ≤ 150 cm) hasta árboles grandes (DAP > 15 cm). Las densidades de tallos fueron más altas en los tipos de bosque sin disturbio y ligeramente perturbados que en los tipos fuertemente y completamente perturbados. La riqueza y la diversidad de especies arbóreas tuvieron sus valores máximos en el bosque ligeramente perturbado. *Acacia mearnsii*, una espercie arbórea introducida en Uganda, fue registrada en el bosque completamente perturbado. La regeneración a partir de rebrotes vegetativos alcanzó su máximo en sitios perturbados, mientras que la regeneración a partir de semillas fue mayor en sitios sin disturbio. El disturbio humano de gran intensidad estuvo asociado con menos signos de daño por mamíferos. El daño que los agentes físicos producen a los árboles y la abundancia de trepadoras se incrementaron con la intensidad del disturbio, excepto en el bosque completamente perturbado. El disturbio humano de gran intensidad afectó negativamente a la abundancia, la diversidad y la regeneración de especies arbóreas, e incrementó la incidencia de daño en los árboles. La regeneración a partir de rebrotes vegetativos fue más importante en sitios fuertemente perturbados. La intensidad del disturbio y la pendiente influyeron sobre la distribución de las especies arbóreas que se están regenerando.

---

[1] *Corresponding Author:* eilu@forest.mak.ac.ug

Resumo: A condição das árvores e as características da regeneração natural das espécies arbóreas foram avaliadas no "Gwindi Impenetrable Forest National Park". A amostragem foi efectuada em tipos florestais não disturbados, levemente disturbados, fortemente disturbados e completamente disturbados. Para determinar as classes de dimensão das árvores, desde as plântulas (diâmetro <2 cm e altura ≤ 150 cm) até grandes árvores (DAP> 15 cm), foram estabelecidas parcelas imbricadas medindo 25x30 m. As maiores densidades de fustes foram encontradas nos tipos florestais não ou ligeiramente disturbados quando postas em confronto com os tipos fortemente ou completamente disturbados. A riqueza específica e a diversidade foram as mais elevadas nas florestas levemente disturbadas. A *Acácia Melanésia*, uma espécie introduzida no Uganda foi registada nas florestas completamente disturbadas. A regeneração a partir de rebentação de toiças era a mais elevada nas estações disturbadas enquanto a regeneração por via seminal era a mais elevada nas estações não disturbadas. Verificou-se também que elevada intensidade de intervenção humana estava associada a poucos sinais de estragos por mamíferos. Os danos em árvores por agentes físicos e abundância de trepadeiras aumentaram com a intensidade dos distúrbios, excepto na floresta completamente disturbada. A elevada intensidade dos distúrbios de origem humana afecta adversamente a abundância das espécies arbóreas, a diversidade e a regeneração e aumenta a incidência das árvores danificadas. A regeneração, a partir de rebentos de toiça, foi mais importante nas estações florestais fortemente disturbadas. A intensidade do distúrbio e o declive influenciou a distribuição das espécies arbóreas em regeneração.

Key words: Albertine rift, human disturbance, regeneration, tropical rain forest.

Introduction

Destruction of natural forest in Uganda during the last two decades has mainly been due to illegal encroachment by agriculturists (Howard 1991). Human disturbance, therefore, contributes to the local variability of forest types in Uganda (Howard 1991). Uncontrolled exploitation has reduced the abundance and diversity of trees in the forest reserves. Bwindi Impenetrable National Park (BINP) has not been an exception to degradation. Successful management and conservation of natural forest requires reliable data on aspects such as the regeneration trends. Although Kakuru (1993) reported the major factors affecting the distribution of the trees in BINP, tree condition, causes of damage or characteristics of tree regeneration have hardly been assessed. The impacts of human disturbance on the forest are not well known. For example, Babaasa (2000) attributed elephant preference for habitats of BINP to seasonality of production and presence of secondary growth. Lejju *et al.* (2001) quantified tree stem density in old croplands of Mgahinga National Park (Uganda), but did not assess tree condition and causes of damage. Although Hubbell *et al.* (1999) argued that strong recruitment limitation appeared to decouple the gap disturbance regime from control of tree diversity in a tropical forest, no distinction was made in the assessment between regeneration from seeds as opposed to regeneration from vegetative sprouts.

This study examined the status of the `regeneration pool' of the tree species in BINP. The main objective was to assess the natural regeneration of tree species in undisturbed, lightly disturbed, heavily disturbed and completely disturbed sites of BINP. Regeneration was assessed in relation to elevation, slope and ground vegetation cover. In addition, tree condition and causes of damage to the trees in the different forest types was assessed. The structure and distribution of the diameter size-classes of the various tree species were assessed. Regeneration from seeds and vegetative re-growth were compared. Disturbance in this context refers to agricultural encroachment, selective timber harvesting and cutting trees of small sizes for non-timber products. The findings of this study will aid future management of BINP and enable identification of key research options.

Materials and methods

Study area

Bwindi Impenetrable National Park (BINP) is located in the Kigezi highlands overlooking the western rift valley in south-western Uganda (0°53'–1°08' S to 29°35'–29°50' E). It covers an area of 331 km^2 and the elevation ranges from 1160–2607 m above sea level. The topography is rugged with numerous steep sided hills and narrow valleys intersected by several rivers. Non-differentiated humic ferralitic soils of poor structure, moderate to high acidity, and deficient in bases occur in the area (Kakuru 1993). The annual rainfall ranges from 1400–1900 mm and the wettest periods are March to April and September to November. The annual mean temperature range is 7–15°C (minimum) and 20–27°C (maximum). The vegetation is classified as medium altitude moist evergreen forest and high altitude submontane forest (Langdale-Brown *et al.* 1964). A total of 223 tree species (53% of Uganda's tree flora) are known from the forest (Kakuru 1993). The fauna includes 22 elephants (*Loxodonta africana*) and other large mammals such as the giant forest hog Hylochoerus meinertzhagene, seven species of diurnal forest primates including the mountain gorillas (*Gorilla gorilla beringei*), and 47 species of small mammals (Howard 1991). About 61% of the forest was heavily exploited by pitsawyers (between 1932 and 1991), 29% was selectively pitsawed and only about 10% remained relatively intact (Howard 1991). Part of the heavily exploited area (10 km^2) was subjected to agricultural encroachment. Wild fires have in the past occurred in some parts of the forest (Butynski 1984). Densely populated (about 230 persons per square kilometre) agricultural lands surround the forest (Obua & Muhanguzi 1998).

Sampling techniques

Based on intensity of past human disturbance, the forest was stratified in terms of proportion of trees above a minimum harvestable size (50 cm dbh) removed by pitsawing as follows: (A) undisturbed forest with 5% removed; (B) lightly disturbed forest with 6 - 70% removed, (C) heavily disturbed forest with more than 70% removed; and (D) completely disturbed forest with more than 31% of land cultivated in the past 15-20 years. Six sample sites: A (Kasiru); B1 and B2 (Nyamugari and Kyangoroka respectively); C1 and C2 (Ruhija and Bamboo respectively); and D (Mbwa River tract) were selected above 1750 m. The dominant tree species at the sample sites A, B1, B2, C1, C2 and D were respectively *Newtonia buchananii*, C*hryosophyllum gorungosanum*, *Chrysophyllum* spp., *Chrysophyllum* spp., patches of *Arundinaria* montane forest and remnants of *Entandrophragma excelsum*, *Chrysophyllum* spp., *Symphonia globulifera* and *Strombosia scheffleri*. The completely disturbed site (D), comprised of degraded forest and post cultivation communities consisting of abandoned gardens of sorghum, millet, maize and tea. The intensity of disturbance decreased towards the less accessible interior of the forest.

Vegetation assessment

Four linear transects 1000 m long and running north, east, south and west were established in each site radiating from a point approximating the centre of the site. Four plots each measuring 25 m x 30 m were established at 225 m intervals on alternate sides of each transect. The total area sampled at each site was 1.2 ha giving a total sample area of 7.2 ha. Trees (excluding bamboo) were enumerated on the basis of diameter class in nested plots measuring 2 m x 5 m (seedlings of diameter < 2 cm and height 0–150 cm); 5 m x 10 m (saplings of diameter 2 – < 5 cm and height > 150 cm); 10 m x 15 m (poles of DBH 5 – < 10 cm); 15 m x 20 m (trees of DBH 10 – < 15 cm); and 25 m x 30 m (trees of DBH ≥ 15 cm). Diameter was measured at breast height (DBH, 1.3 m high) using vernier callipers. Seedling stems were measured at the 'root collar' (ground level).

All trees found in the plots were enumerated and identified using vegetative field characteristics and scientific identification keys of Hamilton (1981) and with the help of experienced botanists at the herbarium in Makerere University. The trees were inspected and their conditions noted using the criteria developed by Alder & Synnott (1992) as seeding or fruiting, defoliated, dead standing, rotting, debarked, fallen, broken branches or broken crown. Causes of damage or death by wind, landslides, insects, mammals, climbers, falling trees, stranglers, fire, felling for non-timber use and logging were also recorded. Stumps were enumerated and the causes recorded. Sprouts from vegetative growth (from roots, fallen stems or stumps) were measured for diameter (of leading shoots). Herbaceous ground vegetation cover (GVC) in the plots was estimated visually and scored as 0–25% (very sparse), 25–50% (sparse), 50–75% (fairly dense), and 75–100% (very dense). Altitude (m) was determined at the origin of transects using an altimeter. Slope position was recorded as upper, mid or lower slope.

Data analysis

The number of species occurring at each sample site (species richness, S) was determined. The Shannon's (H') diversity index (Magurran 1988) was calculated using the formula $H' = -\sum (p_i * \ln(p_i))$, (where p_i is the proportion of individuals found in the i^{th} species. The analysis was carried out using the computer program PC-ORD (McCune & Mefford 1997). Kruskal-Wallis single factor ANOVA by ranks was used to show the difference in stem numbers between sites. Non-parametric multiple comparison was used to show the difference (s) in stem numbers between pairs of sample sites. Detrended Correspondence Analysis (DCA) was used to show the occurrence of species under different intensities of disturbance. Tree species preference for topographic (or slope) positions under different disturbance intensities was also analysed using DCA. The top 10 species from each sample site (in terms of stem densities) in the regeneration (classes < 10 cm DBH) were used in the analyses of tree species preference for slope positions. The Mann-Whitney test was used, for the seedlings, saplings and poles to determine if there were differences in the contributions of regeneration from seeds and from vegetative sprouts.

Table 1. Tree species abundance in 1.2 ha samples of undisturbed (A) and disturbed sites (B, C and D) of Bwindi Impenetrable National Park. Species codes are used in Figs. 4 and 5).

Species name	Family	Code	A	B1	B2	C1	C2	D
Alangium chinense (Lour.) Harms	Alangiaceae	Alachi	5	5	6	28	0	0
Tabernaemontana holstii K. Schum	Apocynaceae	Tabhol	8	10	33	2	0	0
Ilex mitis (L.) Radlk.	Aquifoliaceae	Illmit	2	2	7	6	0	0
Polyscias fulva (Hiern) Harms	Araliaceae	Polful	2	3	4	13	10	10
Schefflera barteri (Seem.) Harms	Araliaceae	Schbar	0	0	11	0	0	0
Ritchiea albersii Gilg	Capparidaceae	Ritalb	1	33	0	16	3	0
Cassine aethiopica Thunb.	Celastraceae	Casaet	1	0	30	0	0	0
Maytenus acuminata (L.f.) Loes	Celastraceae	Mayacu	1	0	0	10	0	0
Maytenus undata Thunb. Blakelock	Celastraceae	Mayund	0	27	3	0	4	0
Parinari excelsa Sabine	Chrysobalanaceae	Parexc	9	3	17	4	0	0
Symphonia globulifera L. f.	Clusiaceae	Symglo	99	6	40	6	5	3
Cyathea manniana Hook	Cyatheaceae	Cyaman	81	15	29	0	0	0
Agauria salicifolia (Comm.) Hook.f.ex Oliv.	Ericaceae	Agasal	0	0	0	31	0	0
Philippia benguelensis (Welw. ex Engl.) Britten	Ericaceae	Phiben	0	0	0	1	0	0
Alchornea sp.	Euphorbiaceae	Alcsp.	1	4	62	8	0	0
Bridelia micrantha (Hochst.) Baill	Euphorbiaceae	Brimic	3	6	6	8	2	13
Cluytia abyssinica Jaub. & Spach	Euphorbiaceae	Cluaby	0	3	0	2	0	0
Croton macrostachyus Hochst. ex Del.	Euphorbiaceae	Cromac	0	5	3	0	0	3
Croton sylvaticus Hochst.	Euphorbiaceae	Crosyl	3	0	0	3	0	0
Drypetes sp.	Euphorbiaceae	Drysp.	27	12	3	1	1	0
Macaranga kilimandscharica Pax	Euphorbiaceae	Mackil	18	17	40	42	40	35
Neoboutonia macrocalyx Pax	Euphorbiaceae	Neomac	5	40	32	14	17	5
Phyllanthus discoideus (Baill.) Webster	Euphorbiaceae	Phydis	4	8	17	0	0	0
Margaritaria sp.	Euphorbiaceae	Physp.	0	0	0	4	0	0
Casearia engleri Gilg.	Flacourtiaceae	Caseng	0	0	7	0	0	0

Contd...

Species name	Family	Code	A	B1	B2	C1	C2	D
Rawsonia lucida Harv. & Sond.	Flacourtiaceae	Rawluc	0	0	9	0	0	0
Harungana madagascariensis Poir.	Guttiferae	Harmad	3	0	2	0	0	0
Ocotea kenyensis (Chiov.) Robyns & Wilczek	Lauraceae	Ocoken	3	0	0	0	0	0
Ocotea usambarensis Engl.	Lauraceae	Ocousa	1	0	0	0	0	0
Newtonia buchananii (Baker) Gilb. & Bout	Leguminosae	Newbuc	182	11	11	4	0	0
Albizia gummifera (J.F. Gmel.) C.A. SM	Leguminosae	Albgum	0	0	0	8	0	3
Erythrina abyssinica Lam. ex DC	Leguminosae	Eryaby	0	0	0	0	0	2
Anthocleista zambesiaca Baker	Loganiaceae	Antzam	1	0	0	0	0	0
Nuxia congesta Fresen.	Loganiaceae	Nuxcon	0	0	0	23	4	0
Memecylon. sp.	Melastomataceae	Memsp.	6	0	0	0	0	0
Entandrophragma excelsum (Dawe and Sprague) Sprague	Meliaceae	Entexc	20	0	17	2	0	4
Bersama abyssinica Fresen.	Melianthaceae	Beraby	0	5	1	3	3	2
Xymalos monospora (Harv.) Warb.	Monimiaceae	Xymmon	7	3	6	31	25	3
Ficus pilosula De Wild.	Moraceae	Ficpil	1	8	0	0	0	0
Ficus sp	Moraceae	Ficsp.	0	0	0	0	2	0
Ficus stipulifera Hutch.	Moraceae	Ficsti	0	2	0	3	0	0
Myrianthus holstii Engl.	Moraceae	Myrhol	1	0	0	1	0	0
Myrica salicifolia Hochst. ex A. Rich	Myricaceae	Myrsal	0	0	0	14	0	2
Maesa lanceolata Forsk.	Myrsinaceae	Maelan	9	8	11	20	7	60
Rapanea rhododendroides (Gilg) Mez	Myrsinaceae	Raprho	68	1	1	2	2	0
Syzygium cordatum Hoschst. ex Krauss	Myrtaceae	Syzcor	18	23	112	2	0	0
Syzygium guineense (Wild.) DC.	Myrtaceae	Syzgui	13	3	3	11	4	0
Strombosia scheffleri Engl.	Olacaceae	Strsch	88	23	69	15	5	6
Olea hochstetteri Baker	Oleaceae	Olehoc	10	3	2	3	0	0
Olinia usambarensis Gilg.	Oliniaceae	Oliusa	30	7	3	24	4	0
Pittosporum spathicalyx De Wild.	Pittosporaceae	Pitspa	2	8	1	38	5	0
Podocarpus milanjianus Rendle	Podocarpaceae	Podmil	428	29	129	49	20	0
Faurea saligna Engl.	Proteaceae	Fausal	5	0	1	33	17	1
Cassipourea sp.	Rhizophoraceae	Cassp.	18	48	92	13	1	0
Hagenia abyssinica (Bruce) J.F. Gnael	Rosaceae	Hagaby	0	0	0	2	0	0
Prunus africana (Hook.f.) Kalkman	Rosaceae	Pruafr	1	1	2	1	2	0
Canthium sp.	Rubiaceae	Cansp.	14	8	5	7	0	0
Coffea eugenioides S. Moore	Rubiaceae	Cofeug	0	0	2	0	0	0
Galiniera coffeoides Del.	Rubiaceae	Galcof	12	0	19	0	5	0
Pavetta sp.	Rubiaceae	Pavsp.	3	0	0	0	0	0
Psychotria megistosticta (S.Moore) Petit	Rubiaceae	Psymeg	13	1	1	3	1	0
Rhytigynia beniensis Blume	Rubiaceae	Rhyben	0	1	2	0	0	0
Rhytigynia kigeziensis Blume	Rubiaceae	Rhykig	1	1	1	8	4	0
Vangueria apiculata K. Schum.	Rubiaceae	Vanapi	0	0	0	0	2	0
Vepris nobilis	Rutaceae	Vepnob	21	1	1	8	0	0
Zanthoxylum macrophylla	Rutaceae	Zanmac	1	2	0	0	0	0
Allophylus macrobotrys Gilg	Sapindaceae	Allmac	4	4	2	5	7	0
Dodonea viscosa Jacq.	Sapindaceae	Dodvis	0	0	0	10	0	0
Chrysophyllum gorungosanum Engl.	Sapotaceae	Chrgor	83	40	275	63	49	8
Dombeya goetzenii K. schum	Sterculiaceae	Domgoe	0	8	2	42	18	4
Ficalhoa laurifolia Hiern	Theaceae	Ficlau	15	0	8	5	0	0
Trema orientalis (L.) BL.	Ulmaceae	Treori	0	2	2	6	6	8

Results

Species richness and diversity

Seventy-two species in 39 families and 63 genera were recorded in the 7.2 ha (Table 1). Euphorbiaceae was the most speciose family with 10 species followed by Rubiaceae (8) and Moraceae (4). There were 24 families with one species each, 10 families with two species each and another two families with three species each. The number of species decreased with intensity of disturbance (51, 50, 48, 45, 30 and 18 species, respectively for sites C1, A, B2, B1, C2 and D). Heavily disturbed site (C1) had unexpectedly high species richness. Species richness in the undisturbed and lightly disturbed sites was about three times higher than in the completely disturbed forest. The lightly disturbed sites had the highest tree species diversity (Shannon's Diversity Index H'=3.42, 3.24, 2.84, 2.83, 2.62 and 2.20, respectively for sites C1, B1, C2, B2, A and D).

Stem density by diameter class

There were significant differences in stem densities between sample sites (H=23.75; P<0.05, Kruskal-Wallis H-test) with higher values for smaller diameter classes than larger classes (Fig. 1). The undisturbed and lightly disturbed sites (A and B2, respectively) had the highest densities of seedlings and larger trees, while heavily and completely disturbed sites (C2 and D, respectively) had the lowest densities for similar diameter classes. There were significant differences in stem densities between undisturbed and lightly disturbed sites on the one part and heavily or completely disturbed sites on the other (A and C2; A and D; B2 and D; B2 and C2; q = 5.08, 4.30, 4.88, respectively and SE=19.69; tabled q=4.03, non-parametric multiple comparison test). There was a significant difference in stem numbers between heavily and completely disturbed sites (q = 4.17, tabled q = 4.03, and SE = 19.69).

Stem density by slope position

Stem density was highest at mid slopes followed by upper slopes (Fig. 2). In the completely disturbed site, the upper slopes had the lowest densities. Densities of small DBH classes were higher on all slopes than larger classes.

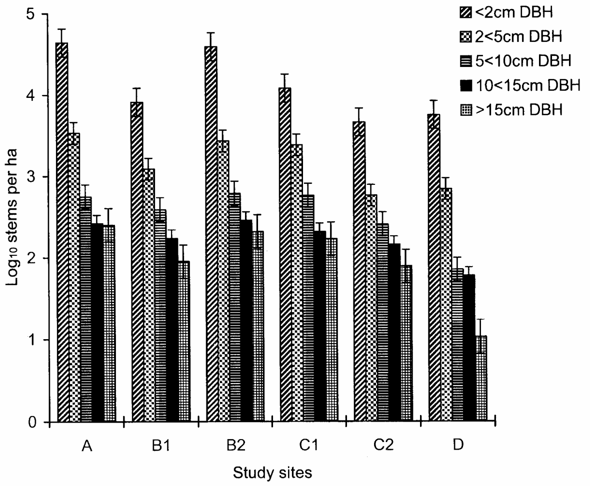

Fig. 1. Stem density by diameter size classes in six sample sites categorised under four intensities of disturbance: Undisturbed forest (A), lightly disturbed forest (B1 and B2), heavily disturbed forest (C1 and C2) and completely disturbed forest (D).

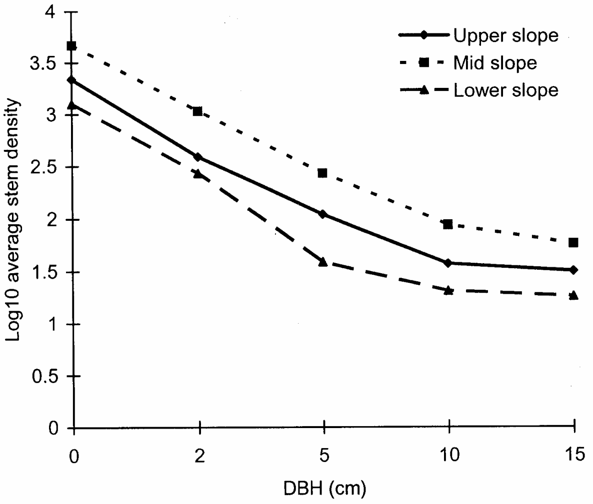

Fig. 2. Stem density of all trees by diameter size-class in the upper, mid and lower slope positions for the undisturbed forest.

Regeneration

Regeneration from vegetative sprouts was dominant in the intensively disturbed sites (Fig. 3). Heavily disturbed site C1 (Fig. 3d) did not conform to the general trend of increased importance of regeneration from vegetative sprouts with intensity of disturbance. There were

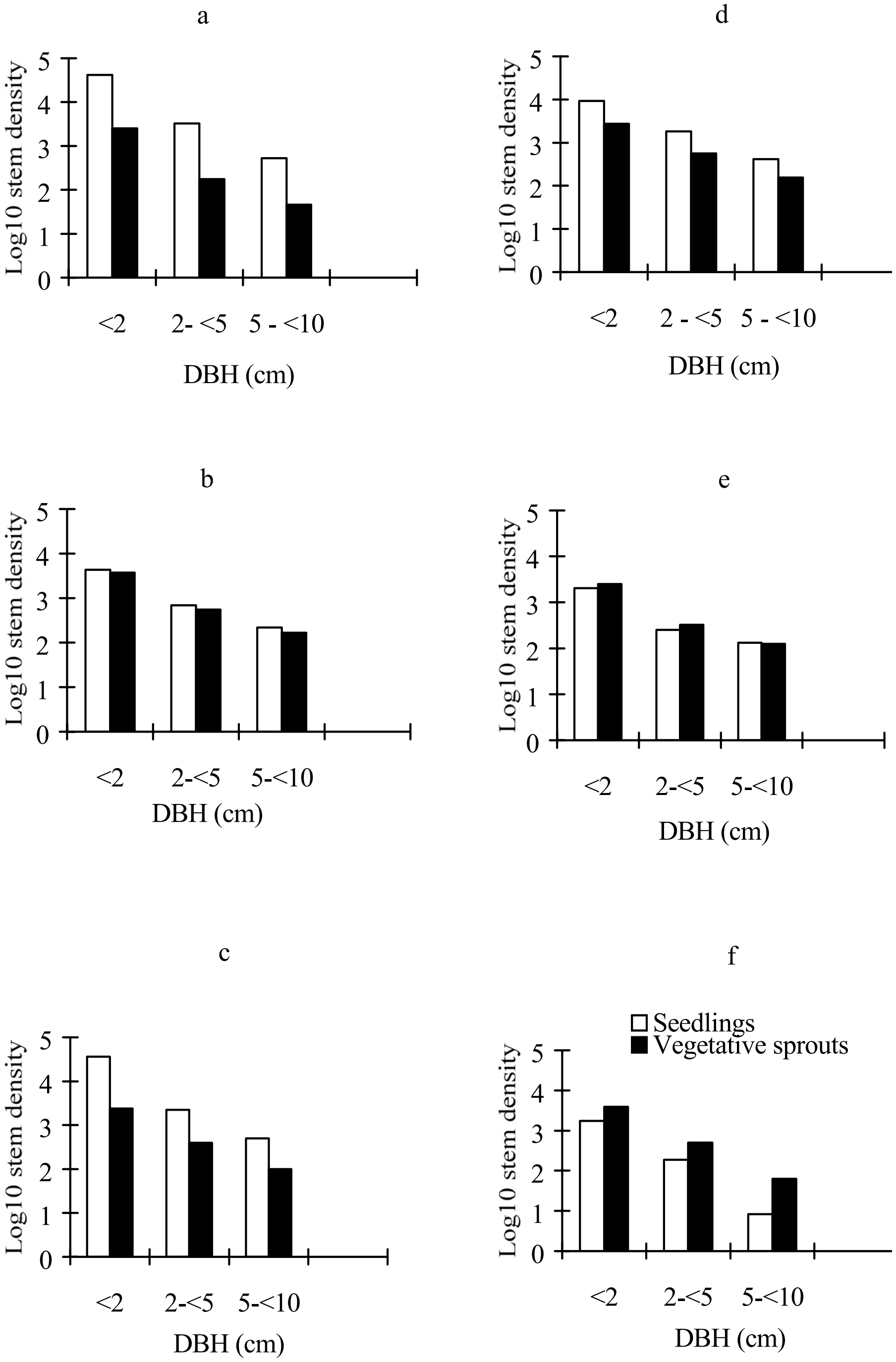

Fig. 3. Proportions of regeneration from seeds and regeneration from vegetative sprouts. a: undisturbed forest (A); b and c, lightly disturbed forest (B1 and B2); d and e, heavily disturbed forest (C1 and C2); and f, completely disturbed forest (D).

significant differences in proportion of the two modes of regeneration in all sites except the lightly disturbed site (B1, Fig. 3b) and the heavily disturbed site (C2, Fig. 3e), (0.001–0.02, $< P(U \geq 181.5–256) < 0.05$; Mann-Whitney U test).The DCA ordination revealed that there was a relationship between tree species distribution and disturbance intensity (Fig. 4). The first two axes of the ordination diagram (axes 1 and 2) respectively explained 35.6% and 44.0% of the cumulative percentage variance of species data (eigenvalues: 0.552 and 0.130) and gradient lengths (3.534 and 1.439) respectively. Axis 1 distinguished species occurring in the undisturbed and completely disturbed sites while the less important axis 2 showed that species found in the lightly and heavily disturbed sites were not clearly distinguishable. The most common tree species found in the undisturbed sites were *Symphonia globulifera*, *Podocarpus milanjianus*, *Newtonia buchananii, Anthocleista zambesiaca* and *Memecylon* sp. Regeneration in the completely disturbed sites comprised of species *Albizzia gummifera, Erythrina abyssinica, Bridelia micrantha, Croton macrostachyus, Macaranga kilimandscharica, Maesa lanceolata, Trema orientalis* and *Polyscias fulva*. Seedlings of *Acacia mearnsii* (not shown in the ordination diagram) were, recorded in the completely disturbed site.

Tree species distribution by slope position

The regeneration of tree species was related to position on the slope (Fig. 5). The first two axes of the DCA ordination diagram, respectively, explained 62.7% and 87.6% of the cumulative percentage variance of species data (eigenvalues: 0.872 and 0.346) and gradient lengths (5.827 and 2.773)

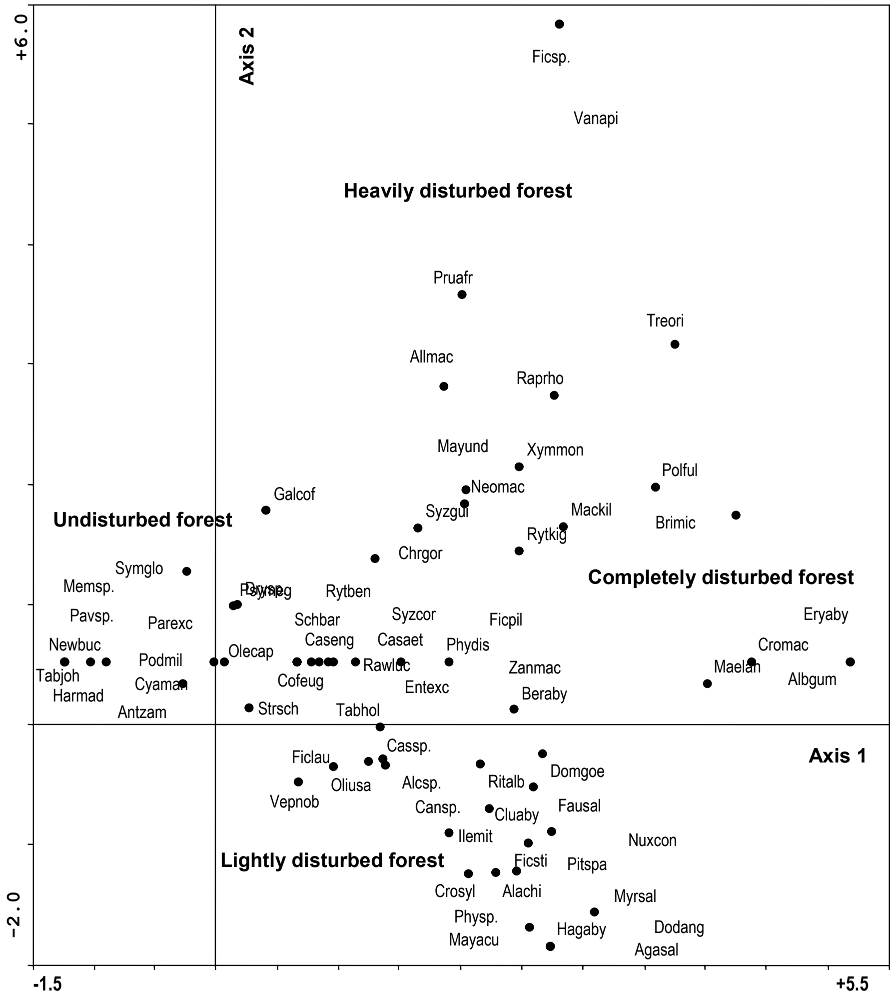

Fig. 4. DCA ordination diagram of tree species distribution in sites of different intensities of disturbance. Species codes are explained in Table 1.

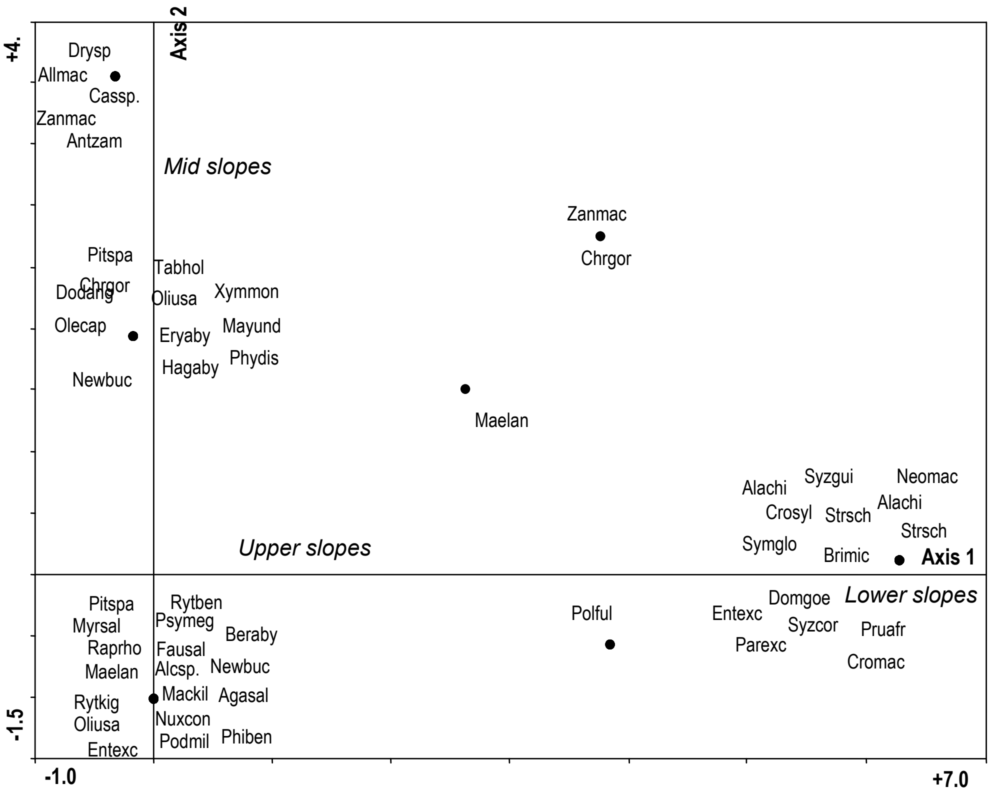

Fig. 5. DCA ordination of tree species and topographic slope position in BINP. Species codes are explained in Table 1.

respectively. Axis 1 distinguished species occurring in the lower slopes from those occurring on the upper and mid slopes. On axis 2, species occurring on upper slopes were separated from those occurring on mid-slopes. *Neoboutonia macrocalyx*, *Dombeya goetzei*, *Bridelia micrantha* and *Croton* spp. occurred most at the lower slopes. In the centre of the ordination diagram, *Phillipia benguelensis*, *Podocarpus milanjianus*, *Olinia usambarensis* and others, occurred and appear to be associated with upper slopes. On mid slopes *Pittosporum spathicalyx* and *Olea hochstetteri* occurred.

Tree condition and causes of damage

Dead standing trees, seeding or fruiting trees and trees with decomposed boles were mainly found in the undisturbed forest (Table 2). The trees were damaged by insects, fungi, and unknown causes. Delimbed, debarked and fallen trees were most abundant in the lightly disturbed forest. Mammals, wind, landslides, and other falling trees damaged trees in undisturbed and lightly disturbed sites. Heavily disturbed sites had trees with broken tops (e.g. *Strombosia scheffleri*). Logging, felling for non-timber use, stranglers and climbers damaged trees in heavily disturbed sites. The completely disturbed site had several defoliated trees and dead or broken stumps. Fires, pitsawing, felling for non-timber use and cultivation damaged trees in completely disturbed sites.

Ground vegetation cover and forest gaps

Ground vegetation cover (GVC) increased with intensity of disturbance (Table 3). Several plots in the undisturbed sites had either sparse or very sparse GVC. Most plots had `dense' to `very dense' GVC in the heavily disturbed site (C1) and completely disturbed site (D). GVC was sparse and much less in the heavily disturbed site C2. Herbaceous plant species such as *Pteridium acquilinium* (L.) Kuhn (Dennstaedtiaceae), *Mimulopsis solmsii* Schweinf. (Acanthaceae) and *Sericostachys scandens* Gilg. & Lopr. (Amaranthaceae) were found mainly in the gaps.

Table 2. Tree condition and causes of damage to trees under the various disturbance intensities in Bwindi Impenetrable Forest. Undisturbed forest (A), lightly disturbed forest (B), heavily disturbed forest (C) and completely disturbed forest (D).

Sample sites	A	B1	B2	C1	C2	D
Tree condition	(in terms of density per ha)					
Seeding or fruiting	46.7	23.3	37.5	30.8	17.5	6.0
Dead standing tree	14.2	7.5	12.5	6.7	4.2	5.0
Rotting tree	8.3	4.2	5.8	4.2	1.7	1.7
Debarked stem	6.7	32.5	15.0	3.3	29.2	1.7
Fallen tree	6.7	14.2	9.2	11.7	13.3	0
Dead/broken stump	5.8	17.5	9.2	76.7	45.0	125.0
Major branches broken	5.0	3.3	5.8	5.0	6.7	0.8
Completely broken crown	4.2	8.3	5.0	16.7	12.5	2.5
Defoliated	0	0	0	0.8	0	1.7
Causes of damage						
Unknown cause of damage	26.7	10.0	20.8	9.2	6.7	1.7
Wind or landslide damage	12.5	9.2	6.7	19.2	14.2	0
Insect damage	10.8	5.0	7.5	3.3	3.3	0
Mammal damage	8.3	35.8	17.5	5.0	33.3	1.7
Climber damage	5.0	8.3	5.0	12.5	10.0	0.8
Damaged by falling tree	5.0	4.2	2.5	7.5	5.8	0
Felled for non-timber use	1.7	8.3	5.0	44.2	28.3	10.0
Strangled tree	1.7	4.2	1.7	6.7	3.3	0.8
Fire damage	0	3.3	0	25.0	20.0	34.2
Sawn stump	0	2.5	0	15.0	5.0	19.2
Logging damage	0	1.7	4.2	10.0	5.8	0

Table 3. Numbers of plots according to ground vegetation cover (GVC) percentages for sample sites in Bwindi Impenetrable National Park

Sample sites (n=16)	Ground vegetation cover			
	Very sparse	Sparse	Dense	Very dense
A: Undisturbed	9	4	2	1
B1: Lightly disturbed	1	3	6	6
B2: Lightly disturbed	5	6	3	2
C1 :Heavily disturbed	3	3	4	6
C2: Heavily disturbed	6	5	5	0
D: Completely disturbed	0	0	6	10

Discussion

Species richness and diversity

Low species richness under high intensity human disturbance has been attributed partly to the effects of high GVC that followed logging (Kasenene 1984). The high numbers of species recorded in undisturbed and the lightly disturbed sites resulted from intermediate levels of disturbance that increased species richness (Hubbel & Foster 1986). In the present study, diversity was lowest in the completely disturbed and the undisturbed sites. Hubbel *et al.* (1999) attributed the increase in species richness with intermediate disturbance to increased stem density in light gaps.

Density by diameter class

The J-inverse diameter distribution of stem density with increasing DBH shows that a small fraction of the seedling and sapling classes survived to the larger tree classes. Kennedy & Swaine (1991) reported two phases of mortality comprising initial mortality which is high, caused by microsite effects or small terrestrial animals, and for the larger DBH classes, competition with other plants that became important and continued as the new plants grew larger. Increased mortality is usually attributed to gap size and light availability, physical damage, soil dryness and herbivore attack (Nunez-Farfan & Dirzo 1989).

Agricultural encroachment depleted trees in the completely disturbed site thus resulting into very low stem densities. Nansen *et al.* (2001) noted that after disturbance, the main trend of change among forest types was related to tree density. In addition, dense GVC developed and suppressed seedling germination and growth. The stem densities recorded in sites under high intensities of disturbance can be explained by catastrophic regeneration characterised by discontinuities in size structure and large patch size (Veblen & Stewart 1980).

Density by slope position

Variation in stem density with slope is partly because of the differences in soil stability and drainage. In BINP rainfall is often high (1400–1900 mm) and the valleys are characterised by damp soils that may suppress regeneration. In addition, Hamilton (1969) noted that valleys were usually open because elephants trampled, uprooted and dug roots of trees. Mountain gorillas in BINP foraged mostly on the lower slopes where herbs and vines were abundant. These factors collectively lowered stem densities on the lower slopes.

Regeneration

Densities of seedlings (originating from seeds) are usually influenced by the densities of large trees some of which are seed trees. Dalling *et al.* (1998) found that seedlings of most species were relatively more abundant than expected in gaps close to their conspecific adults. Other processes that affect seed and seedling production are predation, dispersal and dormancy (Janzen & Vazyuez-Yanes 1991). These processes were not investigated in this study although their role is considered important. The presence of many gaps, dense GVC, and large mammal (e.g. elephant) damage, and lower slopes did not favour regeneration from seeds. Densities of vegetative sprouts were high in disturbed sites because of damage by large mammals and humans induced such regeneration. Acidity of soils (as in the heavily disturbed bamboo zone of BINP, Kakuru 1993) may hinder regeneration from seeds. Janzen & Vazquez-Yanes (1991) noted that isolated trees left as seed sources (in completely disturbed sites) were not necessarily effective seed sources because unfavourable soil conditions and scarcity of pollinators or dispersers curtailed effective reproduction. However, Carrière *et al.* (2002) showed that remnant trees in fields may facilitate regeneration by attracting seed dispersers and creating favourable sites for plant establishment. Re-growth in cleared forest, was therefore, made up of `pioneers' that germinated from seed, surviving seedlings, and sprouts from root and stump sucker shoots (Whitmore 1990). Burning during clearing for agriculture in the completely disturbed sites destroyed the soil seed banks and reduced the number of vegetative sprouts or seedlings.

Species distribution by slope position

Tree species preference for slope types may be attributed to differences in moisture levels (Hamilton 1972). While *Neoboutonia macrocalyx* and *Dombeya goetzenii* occurred at lower slope positions, they were recorded mainly in gaps and are categorised as pioneers or shade-intolerant. Similarly, species recorded in completely disturbed sites were generally light demanders that withstood increased illumination (Whitmore 1990). Regeneration of *Acacia mearnsii*, an introduced species, in the completely disturbed site poses a threat to the indigenous species if it became invasive. Occurrence of *Croton macrostachyus, Macaranga kilimandscharica, Trema orientalis, Erythrina abyssinica* and *Albizia gummifera* in disturbed sites is consistent with a report by Webb (1998) that the importance of shade-intolerant species increased with disturbance.

Tree condition and causes of damage

In the undisturbed forest, Elena *et al.* (1992) reported that the oldest adult trees died standing, apparently due to senescence. Natural tree mortality was caused by shading, strangulation by climbers and age. Natural factors, therefore, damaged trees in undisturbed sites. According to Whitmore (1990), climax tree species in big gaps are often prone to attack by shoot borers, leaf galls, or partial defoliation because of increased stress and reduced resistance. Encroached areas were burnt for agriculture while fires in heavily disturbed sites are lit by hunters and honey gatherers. Such destructive activities need to be closely monitored to avoid extensive damage of the forest. Occurrence of *Agauria salicifolia, Dodonaea viscosa* and *Myrica salicifolia* that are characteristic of woodlands (Morrison & Hamilton 1974) is evidence for frequent fires in some sites in BINP in the past.

Signs of mammal activity were common in the lightly disturbed forest where more food was perhaps available. Variations in food distribution influence ranging patterns of animals. High intensity human disturbance was associated with fewer signs of mammal activity but heavily disturbed Bamboo forest was an exception because elephants frequently feed on shoots of Bamboo (*Arundinaria alpina* K. Schum.) (Babaasa 2000). Janzen & Vazquez-Yanes (1991) reported that in most species-rich tropical forests, animals dispersed seeds of more than 75% of the species of woody plants. Dalling *et al.* (1998) noted that dispersal limitation exerts a considerable effect on seedling distribution. In BINP, baboons and monkeys dispersed the seeds in completely disturbed forest.

The high occurrence of climber infested and strangled trees in the heavily disturbed sites resulted from opening the forest canopy (Lowe &

Walker 1977; Putz 1984). Babweteera *et al.* (2000) found that climber abundance increased with gap size, age and canopy openness. In this study, however, climber abundance in the completely disturbed sites was limited by trellis availability. This is reported to hinder the distribution and abundance of climbers (Balfour & Bond 1993). Heavy disturbance on exposed sites creates large gaps and increases vulnerability of trees to windthrows. Tree falls tend to occur on the edges of pre-existing gaps (Hubbel & Foster 1986) and mortality is usually highest in heavily logged areas (Chapman & Chapman 1997). Dead standing trees were most common in the undisturbed sites.

Gaps and ground vegetation cover

Human disturbance was clearly a major cause of gaps in BINP, the others being large mammals (especially elephants), wind and landslides. The mammals were important in maintaining gaps by their feeding and trampling. This has been reported to be the case for elephants. In Kibale National Park (Uganda), Chapman & Chapman (1997) reported that elephants maintained gaps in the forest. Fires occasionally created large gaps and landslides created small gaps (mainly at the roadsides). The dense to very dense GVC in the gaps, is attributed to increased light penetration that encouraged the growth of luxuriant tangles of herbaceous under storey.

Conclusions

Our results indicate that high intensity human disturbance adversely affected tree species abundance, diversity and regeneration. This was aggravated by increased incidence of damage to trees. Resprouting was the major form of tree regeneration in heavily disturbed sites. The distribution of regenerating tree species was influenced by intensity of disturbance as well as position on the slope.

Restoration of disturbed forest by artificial regeneration may not be required in BINP as it may interfere with the natural regeneration process. As noted by Webb (1998), logging gaps tend to return to pre-logging composition with time under a carefully implemented and controlled harvesting regime. With the exception of the completely disturbed sites, the selectively logged sites approximate 'a controlled harvesting regime'. There is a need to establish permanent sample plots (PSPs) to represent different disturbance intensities and to monitor changes in the regeneration, tree phenology, gap dynamics and spread of introduced species such as *Acacia mearnsii.* Control of crop raiding by baboons should be undertaken cautiously because they help in seed dispersal. Mekuria *et al.* (1999) noted that accumulation of seeds in the soil seed bank in areas far from the parent tree was determined by density of mature trees in the standing vegetation and the mode and adaptation of seed dispersal strategy of the different species. Zoning new multiple-use areas should exclude sites with high mammal activity (e.g. C2) and sites with limited natural regeneration (e.g. D).

Acknowledgements

The study was funded by WWF through the Institute of Tropical Forest Conservation (ITFC) and Makerere University Institute of Environment and Natural Resources (MUIENR). D. Aleper and S. Mugume helped in planning the fieldwork. G. Mayoba and J. Biryomumeisho helped with data collection.

References

Alder, d. & T.J. Synnott. 1992. Permanent sample plot techniques for mixed tropical forest. *Tropical Forestry Papers* 25. Oxford Forestry Institute, Oxford.

Babaasa, D. 2000. Habitat selection by elephants in Bwindi Impenetrable National Park, south-western Uganda. *African Journal of Ecology* **38:**116–122.

Babweteera, F., A. Plumptre & J. Obua. 2000. Effect of gap size and age on climber abundance and diversity in Budongo Forest Reserve, Uganda. *African Journal of Ecology* **38:**230–237.

Balfour, D.A. & W.J. Bond. 1993. Factors limiting climber distribution and abundance in a southern African forest. *Journal of Ecology* **81:** 93–99.

Butynski, T.M. 1984. *Ecological Survey of the Impenetrable Forest, Uganda and Recommendations for its Conservation and Management.* Report to the Uganda Government, Kampala, Uganda.

Carriére, S.M., P. Letourmy, & D.B. Mckey. 2002. Effects of remnant trees in fallows on diversity and structure of forest regrowth in a slash-and -burn agricultural system in southern Cameroon. *Journal of Tropical Ecology* **18:** 375–396.

Chapman, C.A. & L.J. Chapman. 1997. Forest regeneration in logged and unlogged forests of Kibale National Park, Uganda. *Biotropica* **29:** 396–412.

Dalling, J.W., S.P. Hubbel & K. Silvera. 1998. Seed dispersal, seedling establishment and gap partitioning among tropical pioneer trees. *Journal of Ecology* **86:**674–689.

Elena, R., E.R. Alvarez-Bulyla & M. Martinez-Ramos. 1992. Demography and allometry of C*ercropia obtusifolia*, a neotropical pioneer tree - an evaluation of the climax-pioneer paradigm for tropical rain forests. *Journal of Ecology* **80:** 275–290.

Hamilton, A.C. 1969. The vegetation of south west Kigezi. *Uganda Journal* **33:** 175–199.

Hamilton, A.C. 1972. The interpretation of pollen diagram from highland Uganda. *Palaeoecology of Africa* **7:** 45–149.

Hamilton, A.C. 1981. *A Field Guide to Uganda Forest Trees*. Makerere University, Kampala.

Howard, P.C. 1991. *Nature Conservation in Uganda's Tropical Forest Reserves*. IUCN tropical forest series. Gland.

Hubbel, S.P. & R.B. Foster. 1986. Canopy gaps and dynamics of a neotropical forest. pp. 77-96. *In:* M.J. Crawley (ed.) *Plant Ecology*. Blackwell Scientific Publications, Oxford.

Hubbel, S.P., R.B. Foster, S.T. O'Brien, K.E. Harms, R. Condit, B. Wechsler, S.J. Wright & S. De Lao Loo. 1999. Light-gap disturbances, recruitment limitation, and tree diversity in a Neotropical forest. *Science* **283:** 554-557.

Janzen, D.H. & C. Vazquez-Yanes. 1991. Aspects of tropical seed ecology of relevance to management of tropical forested wildlands. pp. 137-157. *In:* A. Gomez-Pompa, T.C. Whitmore & M. Hadley (eds.) *Rain Forest Regeneration and Management*. UNESCO and Parthenon Publishing Group, Paris.

Kakuru, W. 1993. *Major Factors Influencing the Distribution of Tree Species in Bwindi Impenetrable National Park (BINP), Uganda*. M.Sc. Dissertation, Makerere University, Kampala.

Kasenene, J.M. 1984. The influence of selective logging on rodent populations and the regeneration of selected tree species in the Kibale forest, Uganda. *Tropical Ecology* **25:** 175–195.

Kennedy, D.N. & M.D. Swaine. 1991 Germination and growth of colonising species in artificial gaps of different sizes in Dipterocarp rain forest. pp. 357–367. *In:* A.G. Marshall & M.D. Swain (eds.) *Tropical Rain Forest: Disturbance and Recovery*. Royal Society, London.

Langdale-Brown, I., H.A. Osmaston & J.G. Wilson. 1964. *The Vegetation of Uganda and its Bearing on Land-Use*. Government Printer, Entebbe.

Lejju, J.B., H. Oryem-Origa & J. Kasenene. 2001. Regeneration of indigenous trees in Mgahinga Gorilla National Park, Uganda. *African Journal of Ecology* **39:** 65–73.

Lowe, R.G. & P. Walker. 1977. Classification of canopy, stem, crown status and climber infestation in natural tropical forest in Nigeria. *Journal of Applied Ecology* **14:** 897–903.

Magurran, A.E. 1988. *Ecological Diversity and Its Measurement*. University Press, Cambridge.

McCune, B. & M.J. Mefford. 1997. *PC–ORD. Multivariate Analysis of Ecological Data, Version 3.0. MjM Software Design*. Glaneden Beach, Oregon USA.

Mekuria Argaw, Demel Teketay & M. Olsson. 1999. Soil seed flora, germination and regeneration pattern of woody species in an *Acacia* woodland of the Rift Valley in Ethiopia. *Journal of Arid Environments* **43**: 411-435.

Morrison, M.E.S. & A.C. Hamilton. 1974. II. Forest clearance and other vegetational changes in the Rukiga highlands during the past 8000 years. *Journal of Ecology* **62:** 1–32.

Nansen, C., A. Tchabi & W.G. Meikle. 2001. Successional sequence of forest types in a disturbed dry forest reserve in southern Benin, West Africa. *Journal of Tropical Ecology* **17:** 525–539.

Nunez-Farfan, J. & R. Divzo. 1989. Leaf survival in relation to herbivory in two tropical pioneer species. *Oikos* **54:** 71–74.

Obua, J. & G. Muhanguzi. 1998. Farmers' knowledge of indigenous tree cultivation around Bwindi Impenetrable Forest National Park, Uganda. *Indigenous Knowledge and Development Monitor* **6:** 11–13.

Putz, F.E. 1984. The natural history of lianas on Barro Colorado Island, Panama. *Ecology* **5:** 1713–1724.

Veblen, T.T. & G.H. Stewart. 1980. Comparison of forest structure and regeneration on Bench and Stewart Islands. *New Zealand Journal of Ecology* **3:** 50–68.

Webb, L.E. 1998. Gap-phase regeneration in selectively logged lowland swamp forest, north-eastern Costa Rica. *Journal of Tropical Ecology* **14:** 247–260.

Whitmore, T.C. 1990. *An Introduction to Tropical Rain Forests*. Oxford University Press, Oxford.